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THE SOUTHEAST ASIAN FRESHWATER PUFFERFISH GENUS *CHONERHINOS* (TETRAODONTIDAE), WITH DESCRIPTIONS OF NEW SPECIES

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ABSTRACT: The tetraodontid pufferfish genus *Chonerhinos*, restricted to fresh water in Southeast Asia, comprises five species, four of which are described as new. The species differ in adult size, coloration, orientation of squamation, depth of caudal peduncle, size of nasal organ, food habits, and geographical distribution. The most widely distributed, *C. nefastus* n.sp., occurs in southern, western, and northern Borneo, the Malay Peninsula, Thailand, Vietnam, Kampuchea, and Laos; it feeds mainly on fish fin rays and scales, and has a slender caudal peduncle and the smallest nasal organ. *Chonerhinos modestus* (Bleeker, 1850), in western Borneo and Sumatra, with perhaps the most varied diet, is the largest species and has the deepest caudal peduncle. The distinctively colored *C. amabilis* n.sp., with the largest nasal organ, occurs in western Borneo and Sumatra and feeds almost exclusively on large aquatic insects. The two new species *C. silus*, with a moderately deep caudal peduncle, and *C. remotus*, with a slender caudal peduncle, have varied diets including insects, and are known only from northern and northeastern Borneo.

Introduction

The freshwater pufferfish genus *Chonerhinos* currently includes a single species, *C. modestus* (Bleeker, 1850), reported from localities throughout much of Southeast Asia. The nominal species *C. africanus* Boulenger, 1909, known only from the holotype supposedly collected in the interior of the Congo basin, has been identified as a junior synonym of *C. modestus* with incorrect locality data (Roberts 1981; herein). The species formerly known as *C. naritus* (Richardson, 1848), from marine, brackish, and perhaps freshwater habitats along the coasts of the South China Sea and eastern Indian Ocean, has been placed in a monotypic genus, *Xenopterus* (Fraser-Bruner 1943; Tyler 1980; herein).

I undertook this revision because three species of *Chonerhinos* were obtained during my ichthyological survey of the Kapuas basin in western Borneo (Kalimantan Barat, Indonesia) in 1976.

Material Examined and Methods

More than 250 specimens of *Chonerhinos* from throughout the range of the genus were examined during this study. These are deposited in the British Museum (Natural History), London, BMNH; California Academy of Sciences, San Francisco (CAS), including material formerly deposited at Stanford University, Stanford (SU); Field Museum of Natural History, Chicago (FMNH); Muséum Genève, Geneva (MG); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum Zoologicum Bogorense, Bogor, Indonesia (MZB); Musée Royal de l'Afrique Centrale, Tervuren (MRAC); Natural History Museum, Basel (NHMB); Rijks-

museum van Natuurlijke Historie, Leiden (RMNH); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); and Zoological Museum, Universiteit van Amsterdam, Amsterdam (ZMA).

Length of specimens is given as standard length unless total length is expressly indicated, and all proportional measurements are given as times in standard length (SL). Vertebral counts were made from radiographs prepared in the Department of Ichthyology, CAS. Sections of skin anterior and ventral to the pectoral fin were removed with a scalpel and stained in alizarin to facilitate illustration of the scales. Orientation of the scales is also obvious in radiographs and can be observed in whole specimens without special preparation.

Chonerhinos Bleeker

Chonerhinos Bleeker, 1854:259–260 (type-species *Tetraodon modestus* Bleeker, 1850, by subsequent designation of Fraser-Bruner 1943:16).

Chonerhinus Bleeker, 1865:213 (unjustified spelling change).

Designation of Type-species.—Fraser-Bruner (1943) is apparently the first author to have properly designated a type-species for *Chonerhinos*. The original description of the genus is as follows: "*Chonerhinos* Blkr [is gekenmerkt] door trechtervormige verdieping ter plaatse der neusopeningen met verhevene randen, lange rug- en aarsvinnen, zigtbare zijlijn en onegekielden rug . . . van *Chonerhinos* 2 t. w. *Chonerhinos modestus* Blkr = *Tetraödon modestus* Blkr olim (van Borneo, Sumatra), *Chonerhinos naritus* Blkr = *Tetraödon naritus* Richds (van Borneo)." Thus, Bleeker included two species in his original account of *Chonerhinos* and did not indicate a type-species. Hollard (1857) defined *Xenopterus* (type-species *X. bellengeri* = *X. naritus*, by monotypy) in such a way that it excludes *Chonerhinos*, which, however, he did not mention by name. Gill (1892) discussed the nomenclatural history of *Chonerhinos* (and *Xenopterus*) at length but oddly did not mention the lack of a type-species. Jordan (1919:256) incorrectly stated that *Tetraodon modestus* Bleeker is the "orthotype" of *Chonerhinos*, meaning that Bleeker (1854) indicated or distinctly implied that this species is the type-species.

Diagnosis.—*Chonerhinos* and its close relative *Xenopterus* differ from all other tetraodontids in having three lateral line canals on side of body instead of one, two, or none; dorsal fin with 22 or more rays; anal fin with 18 or more rays; at least 24 vertebrae; and prefrontal bones absent (Tyler, 1980). *Chonerhinos* differs from *Xenopterus* in its smaller adult size, less extensive squamation, less exposed olfactory lamellae, and fewer fin rays and vertebrae. The largest *Chonerhinos* I have examined is 106 mm; *Xenopterus* attains at least twice this size. In *Chonerhinos* the scales are relatively small and restricted to the head and body ventral to the level of the pectoral fin; in *Xenopterus* the scales are relatively large and extend dorsally to the pectoral fin. In *Chonerhinos* the olfactory lamellae are largely covered by nasal flaps in broad contact; in *Xenopterus* the nasal flaps are greatly reduced and the olfactory lamellae are consequently almost entirely exposed. *Chonerhinos* has 22–28 dorsal-fin rays, 18–22 anal-fin rays, 13–17 pectoral-fin rays, and 24–28 vertebrae; the same counts in *Xenopterus* are 32–38, 28–29, 18–19, and 29–30.

Remarks.—Tyler (1980) stated that *Chonerhinos* and *Xenopterus* are highly specialized tetraodontids which have secondarily increased the number of dorsal- and anal-fin rays and vertebrae, elaborated the lateral line system, increased the number and size of the olfactory lamellae, and increased the size of at least some of the scales; and that the greater numbers of vertebrae and fin rays in *Xenopterus* as well as the structure of the skull indicates that it is the more specialized of the two. In *Chonerhinos*, according to Tyler, apart from the absence of the prefrontal bones, the skull is not markedly different from that in many species of the tetraodontid genera *Monotreta*, *Chelonodon*, and *Tetraodon*, whereas in *Xenopterus* the frontals are much more laterally expanded and thickened than in *Chonerhinos*, forming a large plate over most of the dorsal surface of the skull, and the supraoccipital crest is wider and heavier; in large specimens the two frontals may become indistinguishably fused to each other in the middle of their lengths (Tyler 1980:340, fig. 274). I have examined two *X. naritus* from Sarawak, BMNH 1894.1.19.86–87, 71.2 and 108 mm. Radiographs reveal that the frontal bones, supraoccipital crest, supraneural bone, anteriormost

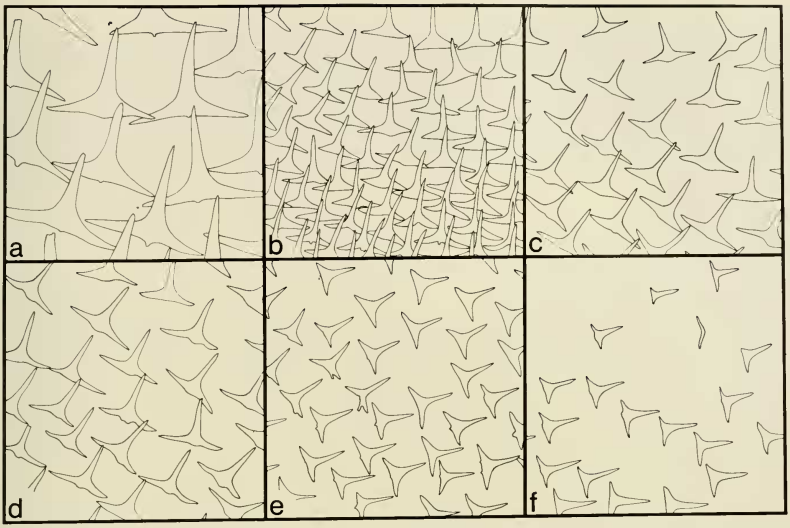

FIGURE 1. Scales on side of body immediately anterior and ventral to pectoral fin (each square = 5 × 5 mm): (*a*) *Xenopterus naritus*, 71.2 mm, BMNH 1894.1.19.86; (*b*) *Chonerhinos modestus*, 48.4 mm, USNM uncatalogued; (*c*) *Chonerhinos silus*, 48.5 mm, FMNH 68815; (*d*) *Chonerhinos remotus*, 49.9 mm, FMNH 68475; (*e*) *Chonerhinos nefastus*, 48.3 mm, CAS 49507; (*f*) *Chonerhinos amabilis*, 48.7 mm, MZB 3973.

anal-fin pterygiophore, and posteriormost neural and haemal spines are enormously thickened or hypertrophied, far out of proportion to neighboring bony elements. They appear to be hyperosteotic (and in the case of the frontal bones, partially synosteotic), and therefore, I am dubious about their phylogenetic significance and their being used as characters to distinguish *Xenopterus* from *Chonerhinos*. Other differences between the two genera, cited above and in Tyler (1980), are sufficient to merit their separation.

Chonerhinos is known only from fresh water. *Xenopterus*, so far as I have been able to determine, is marine or estuarine. There do not seem to be any museum specimens of *Xenopterus* with locality data from fresh water, and statements in the literature that *Xenopterus* occurs in fresh water (e.g., Cantor 1850:384; Weber and de Beaufort 1962:373) appear to be based at least partly on misinformation or confusion with *Chonerhinos*.

In *Chonerhinos* and *Xenopterus*, as in many other tetraodontids, each scale has a spinelike distal portion which projects more or less straight out from the skin when erected, as usually occurs when the fish inflates itself. When the scales are not erect, they are partially or wholly retracted beneath the skin, and the spines may be oriented dorsally, dorsoposteriorly, or posteriorly, depending upon the species (Fig. 1).

Size and shape of the jaw-teeth appear to be nearly identical in all species of *Chonerhinos*. One or two specimens of each species were dissected to permit observation of the gill rakers; all of the species have about 8–10 total gill rakers on each gill arch (sometimes fewer on the first arch). I have not attempted to distinguish the species by differences in the pathways of the lateral line canals. These are difficult to observe in many specimens, and they seem to be highly variable among individual specimens, often being irregularly interrupted or running into each other (Tyler 1980:fig. 223) and frequently differing in their courses on opposite sides of a specimen. Neither have I attempted to distinguish the species by counts of olfactory lamel-

Table 1. Proportional Measurements in *Chonerhinos* (expressed as times in standard length).

	C. amabilis	*C. modestus*	*C. nefastus*	*C. remotus*	*C. silus*
n	20	13	54	31	33
SL mm	35.6–70.4	46.8–106	19.0–70.7	32.8–61.4	32.7–81.8
Eye	7.8–11.2	9.4–14.1	7.2–11.7	8.6–12.0	8.8–12.9
Nasal organ length	10.1–17.9	14.7–25.3	17.3–27.4	12.5–20.1	11.2–20.0
Snout length	6.0–7.2	6.4–7.5	5.8–7.1	6.6–8.7	6.3–8.1
Interorbital width	5.1–6.1	4.6–6.8	4.5–7.0	5.2–7.0	4.9–6.6
Pectoral-fin base length	10.5–12.2	9.5–11.5	9.9–13.5	8.9–11.1	9.1–12.4
Caudal peduncle depth	7.3–8.3	6.7–7.4	7.8–9.9	7.6–9.9	7.2–8.2
Caudal peduncle length	5.0–6.5	5.2–6.4	4.4–5.9	4.6–6.3	4.6–6.5

lae, the number of which seems to be highly variable within each species, as is the size of the nasal organ itself (Table 1).

Proportional Measurements; Meristic Features

Proportional measurements, in most instances broadly overlapping and of little help in distinguishing species, are presented in Table 1. Frequencies of counts of fin rays and vertebrae, diagnostic for the genus but differing slightly among species and of little or no help in identifying individual specimens, are presented in Tables 2–3. Except in a few instances when counts or measurements are particularly useful for definition of species, these data are not repeated in the text.

Key to Species of *Chonerhinos*

1a. Scales on side of body anterior and ventral to pectoral fin with spines directed posteriorly (Fig. 1*e–f*) 2

1b. Scales on side of body anterior and ventral to pectoral fin with spines directed dorsally or dorsoposteriorly (Fig. 1*b–d*) 3

2a. A roundish dark spot in middle of caudal peduncle; dorsal and anal fins always with angulated margins; upper lip not projecting beyond lower lip; exposed portion of eye round; nasal organ relatively large, its length 10.1–17.9 (times in SL) ..... *C. amabilis*

2b. No spot on caudal peduncle; dorsal and anal fins usually with rounded margins; upper lip usually projecting beyond lower lip; exposed portion of eye usually horizontally oval, especially in larger specimens; nasal organ relatively small, its length 17.3–27.4 ..... *C. nefastus*

3a. Depth of caudal peduncle 6.7–7.4; upper and lower lips about equally projecting or lower lip slightly protruding; snout gently sloping; scales on side of body anterior and ventral to pectoral fin, very close-set with spines directed dorsally (Fig. 1*b*); anal-fin rays 20–22, modally 22 (Table 2); adult size to 106 mm ..... *C. modestus*

3b. Depth of caudal peduncle 7.2–9.9; lower lip usually projecting beyond upper lip; snout strongly sloping; scales on side of

Table 2. Frequencies of Fin Ray Counts in *Chonerhinos*.

	Dorsal fin							Anal fin					Pectoral fin				
	22	23	24	25	26	27	28	18	19	20	21	22	13	14	15	16	17
C. amabilis	–	–	1	12	6	1	–	–	–	14	6	–	–	3	16	1	–
C. modestus	–	–	–	4	12	8	1	–	–	1	7	17	–	1	9	14	1
C. nefastus	–	3	23	16	8	4	–	–	1	19	31	3	5	28	20	1	–
C. remotus	5	30	40	8	2	–	–	6	41	37	3	–	–	9	52	26	–
C. silus	–	1	8	18	27	3	1	1	2	19	34	3	–	2	36	15	1

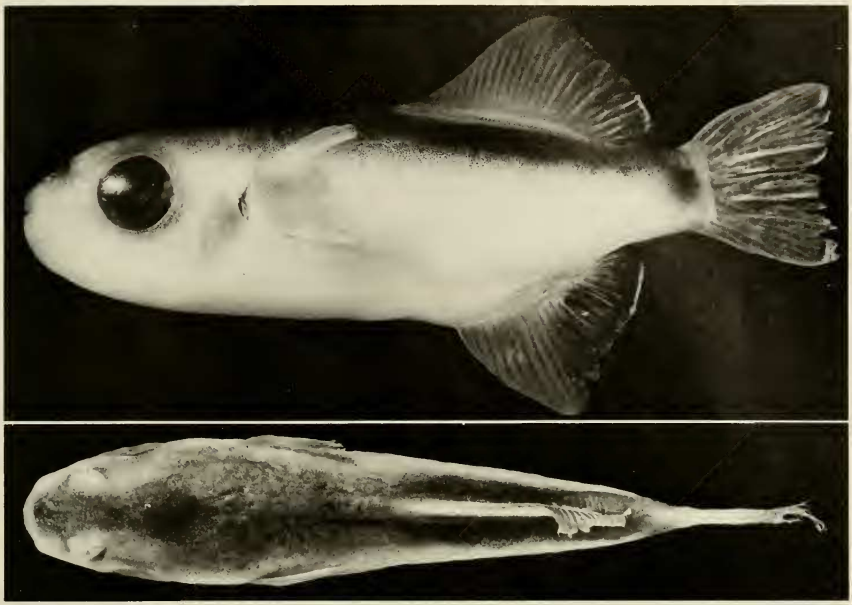

FIGURE 2. *Chonerhinos amabilis*, 45.2 mm, MZB 3972 (holotype).

body anterior and ventral to pectoral fin not as close-set and with spines directed dorsoposteriorly (Fig. 1*c–d*); anal-fin rays 18–22, rarely 22, modally 19 or 20 (Table 2); adult size to 82 mm 4

4a. Caudal peduncle moderately deep, its depth 7.2–8.2; dorsal-fin rays 23–28, average 25.4 ..... *C. silus*

4b. Caudal peduncle slender, its depth 7.6–9.9; dorsal-fin rays 22–26, average 23.6 ..... *C. remotus*

Chonerhinos amabilis new species

(Figure 2)

Chonerhinus naritus WEBER AND DE BEAUFORT, 1962:374 (specimens reported from "Labang hara, soengei Serawai").

Chonerhinus modestus WEBER AND DE BEAUFORT, 1962:fig. 84.

HOLOTYPE.—MZB 3972, 45.2 mm, Kapuas R. 6 km W of Putussibau, Kapuas Ichthyological Survey, 9 Aug. 1976.

PARATYPES.—CAS 49504, 45.0 mm, same data as holotype; MZB 3973, 48.7 mm, Kapuas basin, Sungai Landok at Ngabang, 83 km ENE of Pontianak, Kapuas Ichthyological Survey, 15 July 1976; MZB 3974, 41.8 mm, Kapuas basin, Sungai Pinoh 20–60 km upstream from Nangapinoh, Kapuas Ichthyo-

TABLE 3. FREQUENCIES OF VERTEBRAL COUNTS IN *Chonerhinos*.

C. amabilis	*C. modestus*	*C. nefastus*	*C. remotus*	*C. silus*
		9 + 15 = 24 (1)		
9? + 16 = 25? (1)		9 + 16 = 25 (2)	9 + 16 = 25 (1)	9? + 16 = 25? (1)
			10 + 15 = 25 (3)	10 + 15 = 25 (2)
9 + 17 = 26 (1)		9 + 17 = 26 (1)		
10 + 16 = 26 (9)	10 + 16 = 26 (3)	10 + 16 = 26 (1)	10 + 16 = 26 (8)	10 + 16 = 26 (8)
		10 + 17 = 27 (6)		10 + 17 = 27 (1)
	11? + 16 = 27? (1)		11? + 16 = 27? (2)	11? + 16 = 27? (1)

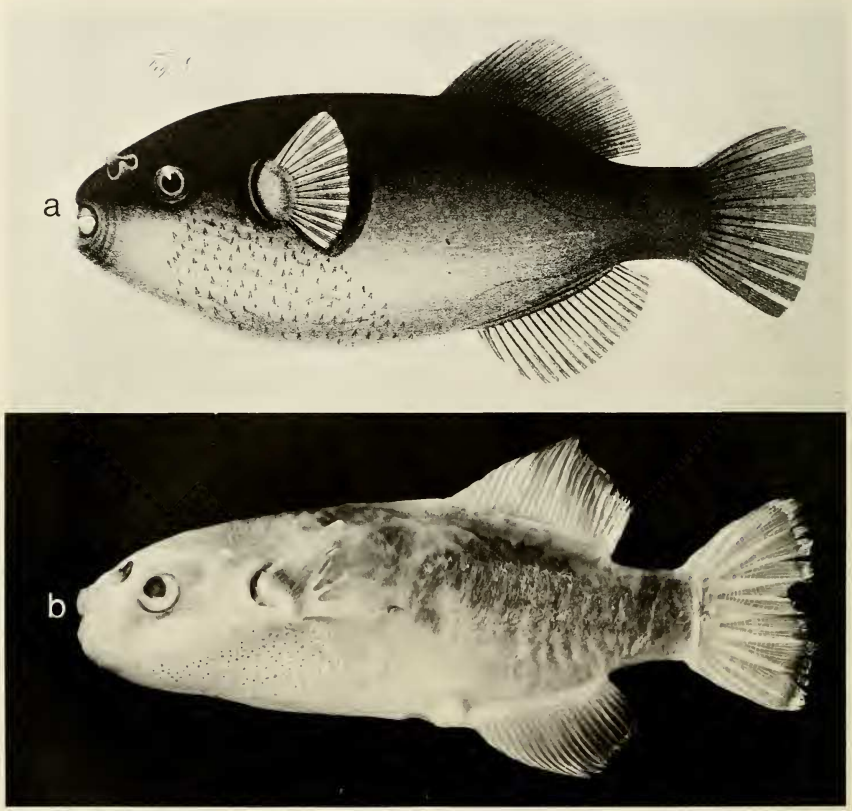

FIGURE 3. *Chonerhinos modestus*: (*a*) as illustrated in Bleeker 1865; length, locality, and present disposition of specimen unknown; (*b*) 78.7 mm, RMNH 26931 (neotype).

logical Survey, 22–26 July 1976; MZB 3975, 38.3 mm, Kapuas R. near Kampong Nibung, 7 km NE of Selimbau, Kapuas Ichthyological Survey, 5–6 July 1976; MZB 3976 and USNM 230359, 2:35.9–36.8 mm, Kapuas R. 53 km W of Putussibau, Kapuas Ichthyological Survey, 6–7 Aug. 1976; MZB 3977 and FMNH 94255, 2:35.6–46.0 mm, Kapuas R. about 23 km WSW of Putussibau, Kapuas Ichthyological Survey, 8–9 Aug. 1976; MNHN 91.216, 36.9 mm, Kapuas basin, M. Chaper, 1890; RMNH uncat., 2:40.9–41.2 mm, Kapuas basin, Sintang, July 1894; RMNH 7935, 4:55.5–68.1 mm, Kapuas basin, Raun, Mar.–May 1894; ZMA 108.912, 3:56.3–70.4 mm, Kapuas basin, Soengai Serawai, Lebang Hara, Witkamp, no date; UMMZ 171708, 2:36.2–38.3 mm, Sumatra, Moesi R. at Moera Klingi, A. Thienemann, 1913.

DIAGNOSIS.—*Chonerhinos amabilis* is readily distinguished from all other members of the genus by its highly distinctive coloration, almost all elements of which are visible in all specimens examined, including some century-old specimens which may have been dead for some time before being preserved. These unique features include a roundish dark spot in middle of caudal peduncle, visible in all specimens; a large, distinctively shaped dark mark on dorsal surface of head extending uninterrupted from just behind upper lip to well behind the eyes, set off by pale coloration on the upper lip, sides of snout, nasal flaps, and skin dorsal to orbits; pale white or milky coloration on ventral and lateral surfaces of body extending very far dorsally; dark col-

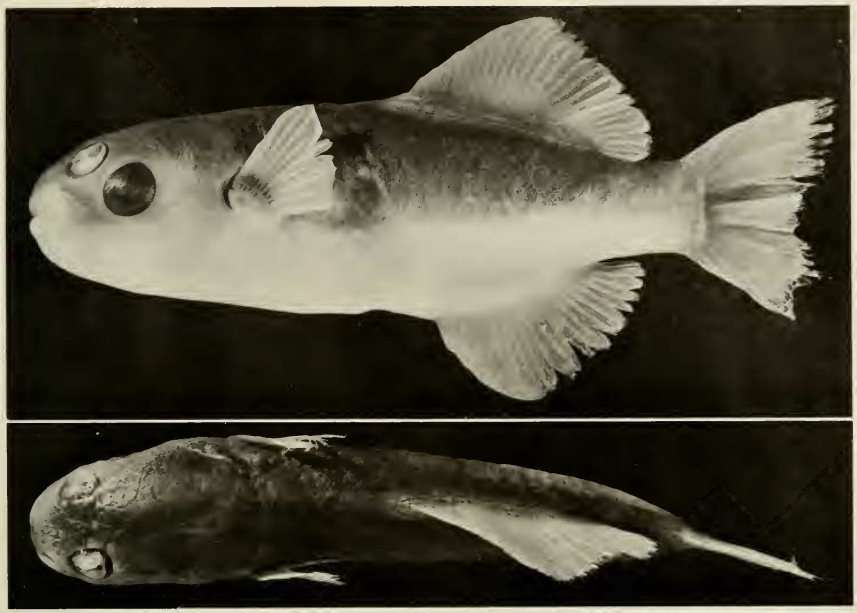

FIGURE 4. *Chonerhinos modestus*, 64.6 mm, CAS 49505.

oration on dorsal surface of body markedly enhanced around base of dorsal fin; and a small dark or dusky oval spot with indistinct margins near tip of chin (very faint or absent in some specimens). In addition, *C. amabilis* tends to have the largest nasal organ of any *Chonerhinos*, and thus of any tetraodontid (Tyler 1980:290); relatively large dorsal and anal fins with angulated (rather than rounded) margins; and scales on side of body anterior and ventral to pectoral fin relatively small, few in number, and with spines directed posteriorly (Fig. 1*f*).

ETYMOLOGY.—Latin *amabilis*, lovely.

Chonerhinos modestus (Bleeker)

(Figures 3–5)

Tetraödon (Arothron) modestus BLEEKER, 1850:16 (type-locality "Banjermassing, in fluviis").

Chonerhinos modestus BLEEKER, 1854:260.

Chonerhinus africanus BOULENGER, 1909:201 (type-locality "riv. Sankuru, à Kondué Kasai, Congo").

NEOTYPE.—RMNH 26931, 78.7 mm, Kapuas basin, Sanggau, Westenenk, 1894.

ADDITIONAL MATERIAL EXAMINED.—RMNH uncat., 2:49.2–59.2 mm, same data as neotype; RMNH 7934, 3:50.0–58.9 mm, Kapuas basin, Sintang, July 1894; CAS 49505 and MZB 3978, 2:64.6–106 mm, Kapuas R. about 23 km wsw of Putussibau, Kapuas Ichthyological Survey, 8–9 Aug. 1976; MZB 3979 and USNM 230360, 2:46.8–48.4 mm, Kapuas R. at Silat, Kapuas Ichthyological Survey, 17 Aug. 1976; BMNH 1846.6.22.75, 86.1 mm, Borneo, Frank Collection, no date; BMNH 1867.11.28.125, 87.3 mm, Borneo, Bleeker Collection, no date; RMNH 12004, 3:66.6–81.1 mm, Sumatra, Lahat, Bleeker Collection, 1850–60; NHMB 822–824, 3:44.7–73.5 mm, Sumatra, Indragiri, H. A. von Meckel, 1895; RMNH 7344 (part only), 8:47.9–62.0 mm, no locality data, Bleeker Collection, no date; MRAC 15306, 52.5 mm, "Congo, Sankuru River, Kasai" (holotype of *C. africanus*).

SELECTION OF NEOTYPE.—Identification of *C. modestus* presented a difficult and taxonomically important problem which I have resolved by selecting a neotype. The holotype is lost or at least it cannot be positively identified, and the original description fits all five species of *Chonerhinos* about equally well. In order to facilitate the following discussion the original description (Bleeker 1850:16) is reproduced here in its entirety:

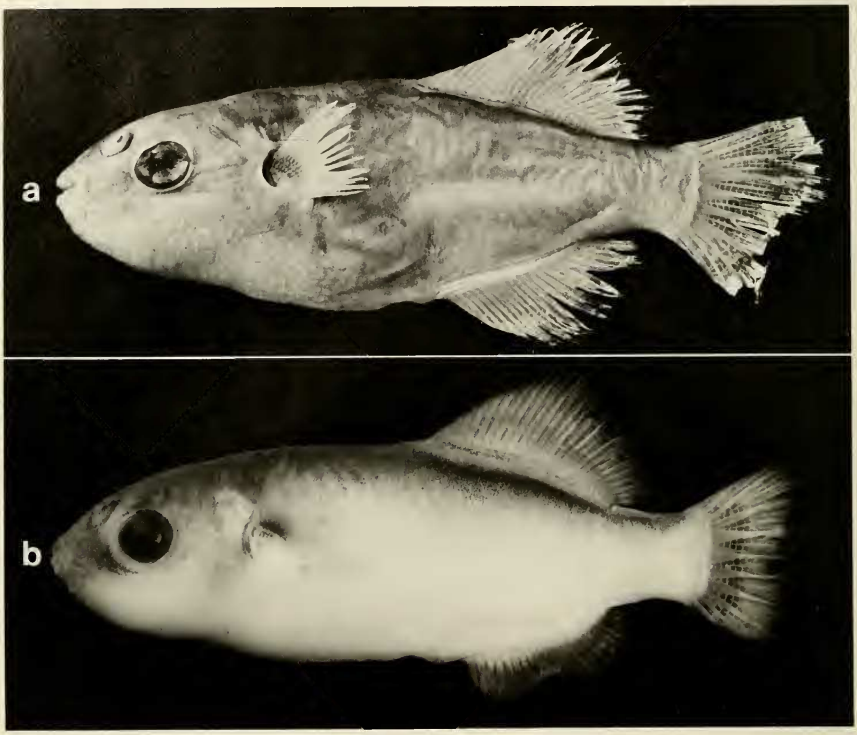

FIGURE 5. *Chonerhinos modestus*: (*a*) 52.5 mm, MRAC 15306 (holotype of *C. africanus*); (*b*) 48.4 mm, USNM 230360.

Tetraödon (Arothron) modestus Blkr.

Tetraöd. corpore oblongo compresso, altitudine 4 circiter in ejus longitudine, latitudine 2 in altitudine; vertice, dorso, lateribus caudaque laevibus, pectore genisque scabris; capite obtuso; lineo rostro-dorsali convexa; maxilla superiore paulo prominente; oculis paulo superis; tentaculis nasalibus 2 conicis obtusis loco narium; linea laterali inconspicua; sacco pneumatico parvo; ano ante pinnam dorsalem sito; pinnis dorsali et anali obtusis angulatis angulis rotundatis, pectoralibus emarginatis, caudali truncata vel leviter emarginata 5 in longitudine corporis; colore corpore supra viridi infra argenteo, pinnis hyalino-viridescente.

D. 5/20. P. 2/12. A. 3/20. C. 9 vel 11 et lat. brev.

Habit. Banjermassing, in fluviis.

Longitudo speciminis unici 60'".

Bleeker almost invariably recorded the length of his specimens as total length in millimeters (pers. commun. M. Boeseman, RMNH). Thus, the last two lines of the description indicate that it was based on a single specimen, the holotype, total length 60 mm, from riverine habitat at Bandjarmasin, southeastern Borneo (Barito basin). Bleeker obtained in all 59 specimens which he identified as *C. modestus*, total lengths 46–126 mm, from Palembang (=Lahat?), Sumatra, and Sambas, Pontianak, and Sintang as well as Bandjarmasin in Borneo (Bleeker 1865:78). All extant "*C. modestus*" from Bleeker's collection apparently are deposited in the BMNH, RMNH, and ZMA. The BMNH and ZMA each have a single Bleeker specimen, both of which are too large to be the holotype: BMNH 1867.11.28.125, 87.3 mm, Borneo, examined by me, and ZMA 102.263, 104 mm, Borneo, examined for me by H. Nijssen. The RMNH has two lots, RMNH 12004, 3:66.6–81.1

mm, Sumatra, Lahat (=Palembang?), and RMNH 7344, 52:29.0–74.0 mm (total lengths 37–88 mm), without locality data. If the holotype still exists, it presumably is in RMNH 7344. Among the 52 specimens are 4 which approximate 60 mm in total length; thus, on the basis of length alone, the holotype cannot be identified. Moreover, each of the four specimens differs by one or two fin rays in at least two of the three counts reported by Bleeker for the dorsal, anal, and pectoral fins of the holotype. In my opinion, none of these specimens can reasonably be identified as the holotype, and since their locality data are lost, a neotype should not be selected from among them. Unfortunately, I have been unable to find any specimen of *Chonerhinos* with locality data from Bandjarmasin or the Barito and do not know which of the species occur(s) there.

As noted above, the original description of *C. modestus* fits all five species of *Chonerhinos* about equally well. All species of *Chonerhinos* normally have 11 caudal-fin rays, and all species are represented by specimens with 25 dorsal-fin rays and 14 pectoral-fin rays. On the other hand, none of the more than 250 specimens examined have 23 anal-fin rays. The highest number of anal-fin rays observed, 22, is usually found in the species herein identified as *C. modestus*, but also occurs in *C. nefastus* and *C. silus*. Coloration and its variation in the species of *Chonerhinos* are too poorly known at present to be of much help in their identification, and Bleeker's description of coloration of the holotype cannot be accepted without reservation since he did not collect the specimen himself and could not have observed it until it had been in preservative for many days or weeks. Bleeker (1865:pl. 213, fig 8) published an excellent figure of a specimen which he identified as *C. modestus*. The length, locality, and date of collection of the specimen figured are not recorded, but it is not the holotype. It is evidently a much larger specimen, with lateral line canals on the body plainly visible, and differs also in fin-ray counts from the holotype as described by Bleeker. I have not tried to match up the figure with an extant specimen, although it may well be part of RMNH 7344. The figure does, however, show a number of features characteristic of the largest species of *Chonerhinos*, with which I unhesitatingly identify it. These features include its large size (indicated by the large size of the published illustration as well as by the relatively small eye); scales with dorsally oriented spines; relatively high counts of dorsal- and anal-fin rays; and deep caudal peduncle. All four specimens of total length 60 mm in RMNH 7344 also belong to this species. Thus, there is every reason to identify it as *C. modestus*, although we cannot be sure that this is the same species obtained for Bleeker at Bandjarmasin. In the absence of specimens with locality data from Bandjarmasin or the Barito, a specimen from the Kapuas basin has been selected as neotype. This specimen bears a strong resemblance to Bleeker's figure of *C. modestus* (Figs. 3*a–b*).

Diagnosis.—*Chonerhinos modestus*, attaining at least 106 mm, apparently is the largest species of *Chonerhinos* and has the deepest caudal peduncle. Depth of caudal peduncle 6.7–7.4 (vs. 7.2–9.9 in all other *Chonerhinos*). Scales relatively large and close-set, those on body anteroventral to pectoral fin with spines directed dorsally, as in *Xenopterus* (vs. spines directed dorsoposteriorly or posteriorly in all other *Chonerhinos*). Upper and lower lips about equally projecting or lower lip slightly protruding. Exposed portion of eye round. Snout gently sloping. Nasal organ moderately large, its length 14.7–25.3. Dorsal-fin rays 25–28; and anal-fin rays 20–22 (generally fewer in other *Chonerhinos*).

Remarks on Synonymy.—Most records of *C. modestus* in the literature other than those cited in the synonymy above refer in whole or in part to other species of *Chonerhinos*.

Chonerhinos africanus was described briefly (and without a figure) on the basis of a single specimen supposedly obtained together with other fish specimens by E. Luja in the Sankuru River, Kasai, Congo basin, in 1908. No additional specimens of *Chonerhinos* have been found in Africa, and the holotype has not been compared previously to *Chonerhinos* from Southeast Asia. I have examined the 52.5-mm holotype (Fig. 5*a*), comparing it directly with specimens of all five species of *Chonerhinos*, and conclude that it is conspecific with *C. modestus*. It has 26 dorsal-fin rays; 22 anal-fin rays; 15 pectoral-fin rays; 10 + 16 vertebrae; scales relatively large, those on sides of body anteroventral to pectoral fin with spines directed dorsally; lower lip slightly protruding; snout gently

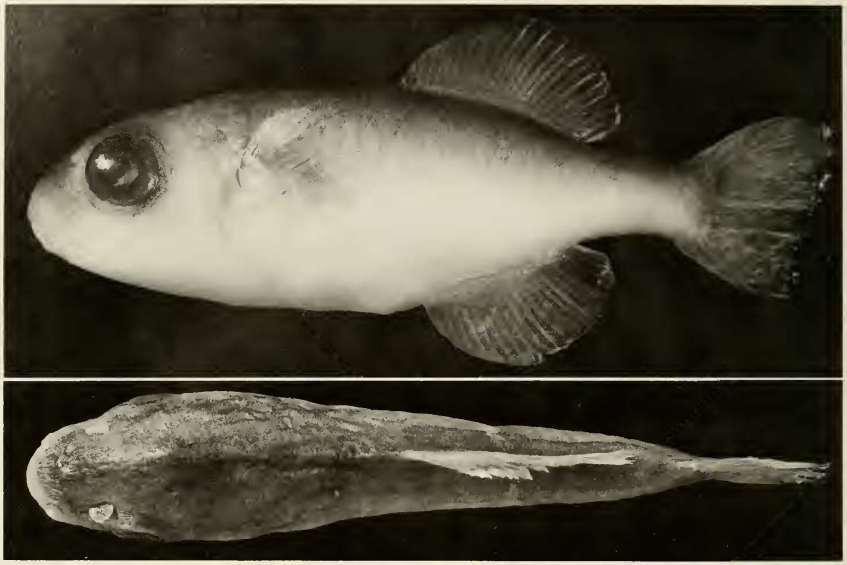

FIGURE 6. *Chonerhinos nefastus*, 47.0 mm, MZB 3980 (holotype).

sloping; eye 10.7; olfactory organ 18.7; snout 7.2; interorbital width 5.25; depth caudal peduncle 7.4; length caudal peduncle 5.9; and pectoral-fin base 10.8. The caudal peduncle depth and anal-fin ray count, while not conclusive, agree best with *C. modestus*. Presumably, the specimen originated somewhere in Southeast Asia and somehow became mixed with Luja's material when it was sent on loan to the BMNH for Boulenger to study.

Chonerhinos nefastus new species

(Figure 6)

Chonerhinos modestus D'AUBENTON AND BLANC, 1966:561 (Mekong basin, Kampuchea); TAKI 1974:199–200, fig. 187 (Mekong basin, Laos); IMAKI et al. 1978:29, pl. 18 (Kapuas R. at Sintang); TYLER 1980 (fig. 223?).

HOLOTYPE.—MZB 3980, 47.0 mm, Kapuas R. 29 km w of Putussibau, Kapuas Ichthyological Survey, 11 Aug. 1976.

PARATYPES.—CAS 49506 and MZB 3981, 4:34.3–43.3 mm, Kapuas R. near Kampong Nibung, 7 km NE of Selimbau, Kapuas Ichthyological Survey, 5–6 July 1976; BMNH 1982.3.29. 254–5 and MZB 3982, 3:36.6–43.7 mm, Kapuas R. 53 km w of Putussibau, Kapuas Ichthyological Survey 6–7 Aug. 1976; IRSNB 632, MZB 3983, ROM 38601, and USNM 230361, 6:32.9–60.2 mm, Kapuas R. about 23 km wsw of Putussibau, Kapuas Ichthyological Survey, 8–9 Aug. 1976; MZB 3984, 51.7 mm, Kapuas basin, small tributary of Sungai Mandai 17 km wsw of Putussibau, Kapuas Ichthyological Survey, 10 Aug. 1976; MZB 3985, 64.9 mm, Kapuas basin, Sungai Mandai Kechil, 18 km wsw of Putussibau, Kapuas Ichthyological Survey, 11 Aug. 1976; CAS 49507 and MZB 3986, 3:36.7–57.8 mm, Kapuas basin, Sungai Tawang near Danau Pengembung, Kapuas Ichthyological Survey, 14–15 Aug. 1976; RMNH 7936, 61.8 mm, Kapuas basin, Sibau, June 1894; RMNH uncat., 25.5 mm, Kapuas basin, Sintang, July 1894; ZMA 110.220, 65.8 mm, Kapuas basin, Bunut, H. A. Lorentz, 26 June 1909; FMNH uncat. 3:38.2–50.1 mm, Sarawak, Niah R., T. Harrisson, 1 Apr. 1963; FMNH uncat., 2:64.8–70.7 mm, Sarawak, Niah, T. Harrisson, no date; FMNH uncat., 3:36.9–41.8 mm, Sarawak, Rejang basin, Baleh R. between Sungai Mujong and Sungai Gaat, R. F. Inger, 3 Aug. 1956; RMNH 7933, 2:56.6–68.0 mm, Mahakam basin, Tepoe, A. W. Nieuwenhuis, 1896–97; MG 2058.94, 34.9 mm, Kalimantan Tengah, Mentaya basin near Sampit, Pfeuffer, May 1980; UMMZ uncat., 50.1 mm, Sumatra, Moesi R. at Moera Klingi, A. Thienemann, 1913; SU 36040, 41.7 mm, Malay Peninsula, Perak, Chandra dam, A. W. Herre, 18 Mar. 1923; UMMZ 197038, 43.7 mm, Thailand, Songkhla Lake off Patalung, K. F. Lagler, 6 Jan. 1965; UMMZ uncat., 48.0 mm, Thailand, Mekong basin, Ubon Ratchtani, Huay Phai, 16 Oct. 1975; UMMZ uncat., 38.9 mm, Thailand, Mekong basin, Ubon Ratchtani, Huay Kwang, 1 Oct. 1976; UMMZ uncat., 42.5 mm, Thailand, Mekong basin, Huay Kwang s of Khong Chiam, Arden, 7 Oct. 1975; UMMZ uncat., 30.9 mm, Thailand, Mekong basin, Mun R. at Khong Chiam, Songrad and Buskirk, 19 July 1975; UMMZ uncat., 3:15.4–32.2 mm, Thailand, Mekong R. and

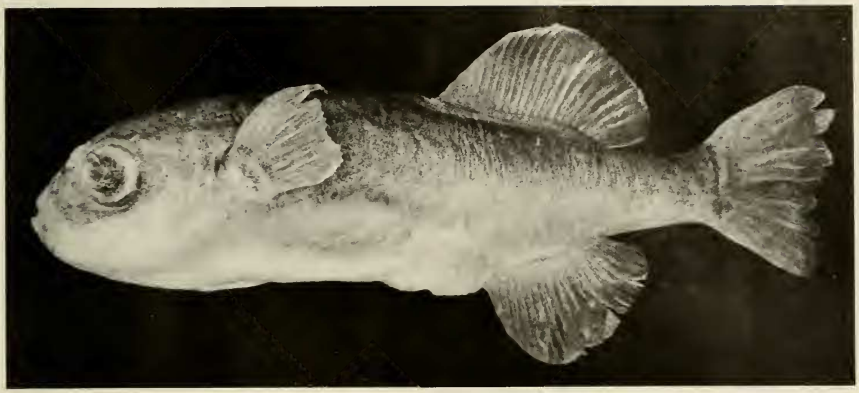

FIGURE 7. *Chonerhinos remotus*, 52.7 mm, FMNH 68475 (holotype).

tributaries from Ban Dan to Nakon Phanom, Mekong fish survey, Mar.–Apr. 1975; MNHN 1966.55–56, 9:21.6–48.1 mm, Kampuchea, Mekong basin, Prek Tasom, F. d'Aubenton, 5 June and 9 Nov. 1961; MNHN 1966.57, 12:19.0–47.5 mm, Kampuchea, Mekong basin, Prek Andor, F. d'Aubenton, 2 Dec. 1961.

DIAGNOSIS.—*Chonerhinos nefastus* differs from all other species of *Chonerhinos* in having upper lip usually projecting beyond lower lip; nasal organ relatively small (Table 1); and exposed portion of eyeball usually horizontally oval rather than round or vertically oval. It differs from all other species except *C. amabilis* in having scales on side of body anterior and ventral to pectoral fin usually with spines directed posteriorly (Fig. 1*e*), and from all except *C. remotus* in its slender caudal peduncle (Table 1). Body usually without distinct color marks except for a slightly darkened spot on dorsal surface of head posterior to eyes.

COMMENTS.—The exposed portion of the eyeball is distinctly horizontally oval in more than half of the specimens examined. It is usually round in very small specimens, however, and sometimes round in large specimens (including the holotype). Most specimens have the scales on the side of the body anterior and ventral to the pectoral fin with the spines directed posteriorly, as in Figure 1*e*. This character is variable, however, and in a few specimens the spines are directed posterodorsally or almost dorsally. This is most noticeable in the sample of 12 specimens from Prek Andor, 4 of which have the spines more dorsally directed than is usual in *C. nefastus*. The rest of the specimens in the sample have the spines directed posteriorly or posterodorsally. Specimens from the Mekong River differ from *C. nefastus* from other localities in having a dark transverse mark on the dorsal surface of the snout between the upper lip and the nostrils.

ETYMOLOGY.—Latin *nefastus*, wicked, abominable, in reference to the food habits (see below).

Chonerhinos remotus new species

(Figure 7)

Chonerhinos modestus HERRE, 1940:55 (Sandakan District, Sungei Segaliud and Sungei Sibuga); INGER AND CHIN 1962:190–191, fig. 101 (Kinabatangan District).

HOLOTYPE.—FMNH 68476, 52.7 mm, Kinabatangan basin, mouth of Sungai Deramakot, R. F. Inger and P. K. Chin, 27 Apr. 1956.

PARATYPES.—FMNH uncat., 9:32.8–54.4 mm, same data as holotype; CAS 49743 and FMNH 68475, 61:29.1–56.8 mm, Kinabatangan R. below mouth of Malubok R., R. F. Inger and P. K. Chin, 25 Apr. 1956; FMNH 68474, 3:47.2–54.4 mm, Kinabatangan R. at Deramakot camp, R. F. Inger and P. K. Chin, 24 Apr. 1956; FMNH 44931, 38.3 mm, Kinabatangan District, N. Borneo Fisheries Dept., 20 Jan. 1949; SU 33487, 2:60.5–61.4 mm, Sandakan District, Sibugal R. (=Sungai Sibuga), A. W. Herre, 19 Apr. 1938; SU 33563, 10:30.5–40.4 mm, Sandakan District, Segaliud R., A. W. Herre, 4 Feb. 1937.

DIAGNOSIS.—*Chonerhinos remotus* is most similar to *C. silus*, from which it differs in having a more slender caudal peduncle (Table 1); fewer dorsal- and anal-fin rays on the average

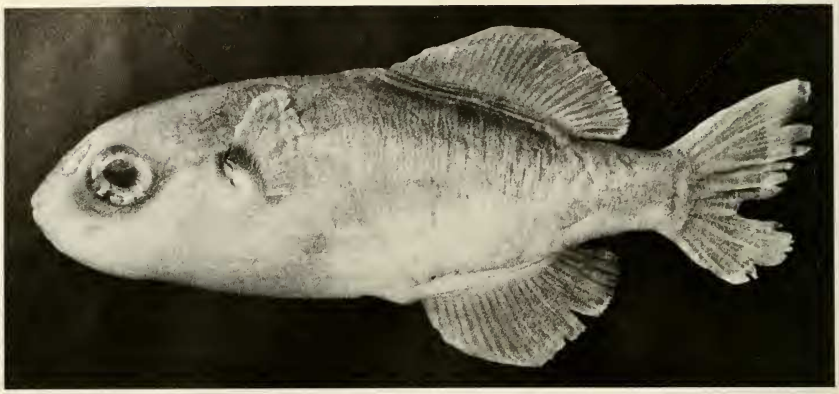

FIGURE 8. *Chonerhinos silus*, 44.9 mm, FMNH 68477 (holotype).

(Table 2); an even more strongly sloping snout; lower lip almost always strongly projecting beyond upper lip (vs. lower lip slightly projecting or equal to upper lip); and eye vertically oval or round (vs. usually round). Scales anterior and ventral to pectoral fin moderately large and close-set, with spines directed posterodorsally (Fig. 1*d*). No distinctive color marks except for a well-defined dark blotch on dorsal surface of head posterior to eyes.

ETYMOLOGY.—Latin *remotus*, remote, in reference to the type-locality.

Chonerhinos silus new species

(Figure 8)

HOLOTYPE.—FMNH 68477, 44.9 mm, Sarawak, Rejang basin, Sungai Baleh between Sungai Mujong and Sungai Gaat, R. F. Inger, 3 Aug. 1956.

PARATYPES.—CAS 49744, FMNH uncat., 36:35.0–60.1 mm, same data as holotype; FMNH 62987, 44.0 mm, Sarawak, Niah R., Niah, Lord Medway, 22 Aug. 1959; FMNH 68813, 81.8 mm, Sarawak, Niah, T. Harrisson, no date; FMNH 68814; 2:44.1–68.7 mm, Sarawak, Niah, Niah R., Pengkalan Lobang, T. Harrisson, 2–11 Nov. 1960; FMNH 68815, 16:37.1–72.9 mm, Sarawak, Niah R., T. Harrisson, 1 Apr. 1963; SU 33610, 32.7 mm, Sarawak, 16 miles [ca. 26 km] E of Kuching, A. W. Herre, 16 Feb. 1937.

DIAGNOSIS.—*Chonerhinos silus* is most similar to *C. remotus* and *C. modestus*. Differences between *C. silus* and *C. remotus* are set forth above in the diagnosis of *C. remotus*. It differs from *C. modestus* in attaining smaller adult size (largest specimen examined 82 mm vs. 106 mm); snout more strongly sloping; lips equally projecting, or lower lip variably protruding, frequently much more so than in *C. modestus*; scales anterior and ventral to pectoral fin with spines projecting dorsoposteriorly (Fig. 1*c*) rather than dorsally (Fig. 1*b*); and caudal peduncle relatively slender, its depth 7.2–8.2 (vs. 6.7–7.4). *C. silus* tends to have fewer dorsal-, anal-, and pectoral-fin rays than *C. modestus* (Table 2), but the counts are broadly overlapping and of little help in identifying individual specimens to species.

ETYMOLOGY.—Latin *silus*, pugnosed.

COLORATION IN LIFE

Most of the specimens of *Chonerhinos* collected during the 1976 Kapuas Ichthyological Survey were caught at night and preserved before their coloration in life could be properly observed. Colors of the 106-mm *C. modestus*, gill-netted at night and removed the next morning, are recorded in my field notes and in a 35-mm Kodachrome slide. It was pale blue dorsally, white on the sides and abdomen, and with a reddish eye. It is my impression that the three smaller *C. modestus* collected during the survey were similarly colored. *C. amabilis* is described in my field notes as lime-green dorsally, with a darkened area along the base of the dorsal fin, and a reddish eye; the round spot on the caudal peduncle, so evident in preserved specimens, was not observed during life (at least it is not recorded in my field notes, and I do not recall

having seen it in the live specimens). I suspect that some *C. amabilis* were blue dorsally but this is not recorded in my field notes. My impression is that all *C. nefastus* caught during the survey were pale green dorsally; at least this was so in several specimens observed during the day. I doubt that any of them were blue dorsally. D'Aubenton and Blanc (1966) reported coloration of *C. nefastus* (as *C. modestus*) from the Mekong basin in Kampuchea as green on the back and white on the flanks and belly, while Taki (1974) reported specimens from the Mekong in Laos as having "back and upper surface of head and body olivaceous golden, underside pale yellow to white. Dorsal and caudal fins greenish yellow; anal fin pale yellow; pectoral fins hyaline."

Sexes

Secondary sexual dimorphism is unknown in *Chonerhinos*. I have examined ripe males and gravid or ripening females in all five species. Ovaries of the left and right sides are about equally well developed. The following approximate counts of eggs and measurements of egg diameters contained in the right ovary were made; *C. amabilis*, 57.4 mm, 180 eggs, 1.1–1.9 mm; *C. modestus*, 106 mm, 800 eggs, 1.5–2.1 mm; *C. nefastus*, 56.5 mm, 100 eggs, 1.4–1.5 mm, 57.8 mm, 80 eggs, 1.3 mm, and 64.9 mm, 230 eggs, 1.3–1.6 mm; *C. remotus*, 54.2 mm, 85 eggs, 1.9–2.3 mm; and *C. silus*, 58.7 mm, 200 eggs, 1.5–2.1 mm. All of these specimens are gravid except the three *C. nefastus*, which are nearly ripe. In *C. remotus* I observed two gravid females, 54.2 and 54.4 mm, and three spent females, 48.8, 51.4, and 52.7 mm (the holotype, Fig. 7), with genitoanal areas much swollen. Such swelling, perhaps present only in females just before or after spawning, has not been observed in other species.

Food Habits

Food habits of *Chonerhinos*, determined by complete or partial examination of gut contents in more than 100 specimens, may be summarized as follows: *C. amabilis* feeds almost exclusively on large aquatic insects; *C. modestus* feeds mainly on terrestrial insects, shrimps, seeds, and to a less extent on whole fish, fin rays, or scales; *C. nefastus* feeds mainly on fish fin rays and scales, and to a lesser extent on insects (aquatic and terrestrial); *C. remotus* and *C. silus* feed mainly on insects aquatic and terrestrial), but also ingest vegetable matter and other items. No fish remains were found in *C. amabilis*, *C. silus*, or, excepting a single fish scale in one specimen, *C. remotus*. Pieces of clam flesh and gills were found in several *C. silus*, and numerous small, whole clams in a single *C. nefastus*, but otherwise molluscs were absent. The food of the five species may be described in more detail as follows.

In *C. amabilis*, 18 of 20 specimens contained more or less abundant remains of insects, mainly large aquatic forms; partial examination of the gut contents of these specimens failed to reveal any other food items. Of the remaining two specimens, one contained moderate amounts of an unidentified flocculent material, and one had empty guts. This species is noteworthy in that nearly all individuals had much food in their guts, and in being the most stenophagic of any species of *Chonerhinos*. In *C. modestus*, guts were examined in 10 specimens, half of which had empty guts. Of the remaining five, four contained moderate to large amounts of insects (mainly terrestrial), two had prawns, two had seeds, two had fish scales, one had fish fin rays, and one had the remains of a small whole cobitid fish (identified by its Weberian apparatus). The last *C. modestus*, the 106-mm specimen, is of particular interest because of its large size and because of the circumstances of its capture. It was gill-netted together with a large catfish, *Pangasius polyuranodon* (Fig. 9), which had much of its abdominal wall and portions of its anal and caudal fins and caudal peduncle bitten away. I suspected that part of the damage may have been done by the *C. modestus*, but careful examination of its gut contents failed to reveal any material from the *Pangasius*. While the *C. modestus* may have regurgitated, its stomach did contain other food items, and it seems more likely that the *Pangasius* was ravaged by some other predator, possibly *C. nefastus*. Of 31 *C. nefastus* in which the gut contents were examined, 11 had more or less substantial amounts of fish fin rays, six had fish scales, three contained small pieces of fish flesh, six had small to moderate amounts of insects (terrestrial and aquatic), two had unidentified debris or detritus, one had numerous small, whole bivalves, and one had a large amount of sand and grit; seven had

FIGURE 9. An 106-mm *Chonerhinos modestus* gill-netted together with an 80-cm *Pangasius polyuranodon* catfish ravaged by an unknown predator, possibly *C. modestus* or *C. nefastus* (Kapuas River near Putussibau).

empty guts. The Latin name *nefastus* refers to the predominantly pterygophagous and lepidophagous habits of this species. Inger and Chin (1962:191) reported gut contents of 11 *C. remotus* (as *C. modestus*) as follows: bits of leaves (6); parts of terrestrial insects (6); Plecoptera nymphs (3); Trichoptera larval cases (1); unidentified insect larvae (3); Acarina (2); unspecified parts of fishes (2). Of 21 *C. remotus* I examined, 18 had guts containing food items: 14 with insects (aquatic and terrestrial), 4 with parts of higher plants, 1 with a mite, 1 with a fish scale, and several with unidentified debris or detritus. In 33 *C. silus*, 22 had guts containing insects (aquatic and terrestrial), 6 contained higher plant material (fine rootlets, leaf, seeds, or seed pulp?), 1 had several pieces of a large, spinulose oligochaete, and 1 had chunks of spiny or hairy flesh (mammalian?); the remainder had empty guts.

Intraspecific Biting

Intraspecific biting, although infrequently documented, probably occurs in many members of the family Tetraodontidae. In *Fugu niphobles* (Jordan and Snyder, 1901), biting is an integral part of spawning behavior: egg laying occurs on the beach at high tide after a female has been bitten on the sides by two to four males (Uno 1955). Many of the specimens of *Chonerhinos* examined exhibited characteristically shaped bite marks on the flanks and, even more frequently, had portions of the median fins bitten off. I suspect that much of the biting, at least in *C. nefastus*, is inflicted by conspecifics. More than half of the specimens examined of this species had bite marks on the flanks or had portions of the dorsal, anal, or caudal fins missing. In many specimens these fins appear to have been bitten repeatedly, as evidenced by scar tissue and imperfect regeneration of fin rays. It is noteworthy that this species feeds predominantly upon fish fin rays (see above under Food Habits). *C. modestus* and *C. silus*, both of which occur sympatrically with *C. nefastus*, also exhibit high frequencies of specimens with bite marks and bitten fins, but it is unclear whether this is a result of intraspecific attacks, attacks by *C. nefastus*, or a combination of both. In all three species the bite marks and fin damage appear to be about equally distributed between the sexes, and between gravid and nongravid females. None of the specimens of *C. amabilis* and *C. remotus* examined exhibited bite marks on the flanks, and their fins were relatively undamaged, with little or no indication of fin-nipping. Perhaps the generally pterygophagous and lepidophagous feeding behavior of *C. nefastus* was preceded by the evolution of an exceptionally aggressive intraspecific biting and fin-nipping behavior.

Geographical Distribution

Tetraodontidae is the only one of the nine families of the large order Plectognathi or Tetraodontiformes which has representatives that occur in fresh water. About 25 of the approximately 140 described tetraodontid species are

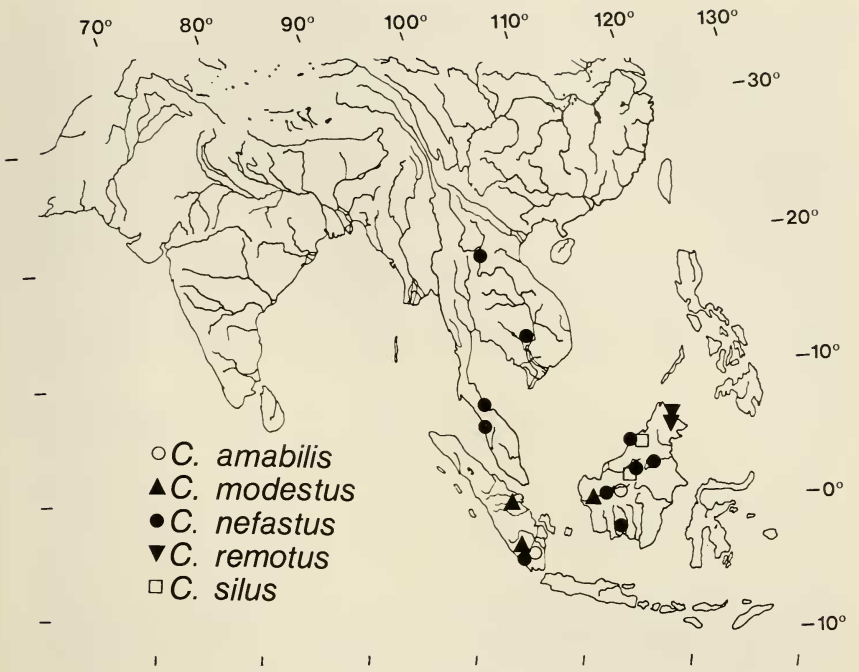

FIGURE 10. Geographical distribution of species of *Chonerhinos*.

endemic to fresh water. *Carinotetraodon* and *Chonerhinos*, both from Southeast Asia, are the only tetraodontid genera restricted to fresh water. Other genera with freshwater species include *Tetraodon* or *Monotreta* in India, Southeast Asia, and New Guinea; *Tetraodon* in Africa; and *Colomesus* in South America. Two features of the geographical distribution of freshwater Tetraodontidae merit comment. First, although marine tetraodontids extend into high latitudes in the Northern and Southern hemispheres, freshwater species occur only within tropical latitudes. Second, the tropical rivers with endemic tetraodontids generally have rich ichthyofaunas dominated by primary freshwater fishes.

Geographical distributions of the species of *Chonerhinos*, based mainly on material examined in this study, are illustrated in Figure 10. Two of the species, *C. amabilis* and *C. modestus*, have distributions lying within the hydrographic limits of the ancient Central Sundaland River basin, now fragmented by the Java and South China seas. I suspect that *C. modestus* also occurs in Thailand but have not examined specimens from there. The most widely distributed species, *C. nefastus*, occurs throughout the area occupied by the Central Sundaland River basin; it also occurs in northern and southern Borneo and in the Mekong basin. Whether the Mekong River once also formed part of the Central Sundaland drainage is a matter under investigation. *C. silus* and *C. remotus*, in northern and northeastern Borneo, have restricted distributions entirely outside the limits of the Central Sundaland drainage area. *C. amabilis*, *C. modestus*, and *C. nefastus* occur sympatrically in the Kapuas River and probably also in some rivers in Sumatra including the Indragiri and

Moesi. *C. nefastus* and *C. silus* occur sympatrically in Sarawak (Rejang and Niah basins).

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